

## **Anthropogenic influence on coastal phytoplankton seasonality**

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### **ABSTRACT**

The effects of temperature and anthropogenic influence on the seasonal distribution and size structure of coastal phytoplankton were studied at two coastal sites in SE Tenerife, Canary Islands. We hypothesized that the anthropogenic influence would shift the trophic state of the system towards more eutrophic levels. The sites had different levels of anthropogenic influence and the sampling was carried out during two time periods with different mean surface temperatures: October 2003 - April 2005 showed higher temperature than February 2007 - April 2008. The more anthropogenically influenced station showed higher phytoplankton production and biomass, due to the higher productivity and biomass of the bigger than two micrometer cells. Two distinct production blooms were detected: a typical late winter bloom which occurred in January – February, and an autumn bloom in October. Photosynthetic picoplankton primary production was higher during the “cold” period compared to the “warm” period, but this production was uncoupled with biomass. Anthropogenic influence produced a more eutrophic state, with decreased importance from picoplankton cells on biomass.

**Keywords:** Phytoplankton; primary production; biomass; coastal waters; Canary Islands.

### **RESUMEN**

Se estudió el efecto de la temperatura y la influencia antrópica sobre la distribución estacional y la estructura de tallas del fitoplancton costero en dos localidades del Sureste de Tenerife, islas Canarias. La hipótesis que planteamos fue que la influencia antrópica modificaría el estado trófico del sistema hacia valores más eutróficos. Las localidades se escogieron por presentar distintos niveles de influencia humana y los muestreos fueron realizados durante dos periodos de tiempo con temperaturas medias superficiales diferentes: de octubre de 2003 a abril de 2005 con una media de temperatura superficial de la mar más alta que la de febrero de 2007 a abril de 2008. El lugar con mayor influencia antrópica

mostró más biomasa y producción del fitoplancton, debido principalmente al aporte de la fracción superior a 2 micrómetros de tamaño. Se detectaron dos picos de producción: uno a finales de invierno, que ocurrió de enero a febrero, y un pico otoñal en octubre. La producción primaria del picoplancton fotosintético fue más alta durante el periodo frío en comparación con el cálido, pero esta producción no se vio relacionada con la biomasa. La influencia antrópica provocó unas condiciones más eutróficas, con una reducción del aporte de las células del picoplancton a la biomasa total del fitoplancton.

**Palabras clave:** Fitoplancton; producción primaria; biomasa; aguas costeras; islas Canarias.

## 1. INTRODUCTION

Phytoplankton is the main primary producer in most marine ecosystems and its size structure is a key factor in modulating the food web dynamics and the carbon cycle (AZAM *et al.* 1983; LEGENDRE & LE FÈVRE, 1991). Photosynthetic picoplankton (ppp), small cells less than 2 mm in size (SIEBURTH *et al.* 1978), is of great importance in marine ecosystems. The ppp is an important component of the pelagic community in both freshwater (HAWLEY & WHITTON, 1991; PETERSEN, 1991; VÖRÖS *et al.* 1991) and marine environments (TAKAHASI *et al.* 1985; ITURRIAGA & MARRA, 1988). It has been established that the contribution of ppp to carbon fixation ranges from 1 to 90% of the total primary production in marine environments (STOCKNER, 1988) and that its contribution to total global aquatic net primary productivity is at least 10% (RAVEN, 1998). The importance of ppp is highest in oligotrophic waters where small phytoplankton cells are responsible for more than 50% of biomass and primary production (AGAWIN *et al.* 2000). In coastal eutrophic waters ppp is less important as phytoplankton structure is dominated by larger cells (JOINT *et al.* 1986; SONDERGAARD *et al.* 1991). However, there is evidence that the microbial food web is an essential feature in coastal upwelling areas in addition to oligotrophic regions (VARGAS & GONZALEZ, 2004). Previous studies have stated that the importance of picoplankton declines as total autotrophic production and biomass increases and that picoplankton biomass and production hold greater importance in warm nutrient-poor waters (AGAWIN *et al.* 2000). POLAT *et al.* (2005) found that temperature was one of the most important factors influencing phytoplankton and that a positive significant correlation existed between temperature and phytoplankton abundance. It is known that microzooplankton grazing activity is the main source of phytoplankton mortality in open ocean (CALBET & LANDRY, 2004). In coastal areas a number of different factors may affect the temporal and spatial distribution of phytoplankton including nutrient availability, light, temperature, turbulence and grazing. In coastal areas nano- and microplankton usually dominate biomass and production for considerable periods of time (MALONE *et al.* 1991; IRIARTE & PURDIE, 1994). However, studies specifically designed to investigate phytoplankton size distribution in shallow oligotrophic waters are scarce. One such study in coastal waters of the Canary Islands (~40 m depth) showed that picoplanktonic cells dominated the phytoplankton (>60% of the primary production) (ARISTEGUI *et al.* 2001).

The Canary Islands region is described as oligotrophic and has a low nutrient concentration, primary production rate and phytoplankton biomass throughout most of the year (DE LEÓN & BRAUN, 1973; BRAUN, 1980; ARÍSTEGUI, 1990). Like in other subtropical areas, a temporal thermocline forms which restricts the vertical flux of nutrients from deep waters to the surface, thus limiting phytoplankton growth. This thermocline is eroded at the end of winter, when surface waters are cooler allowing mixing of deep nutrient rich waters with the nutrient depleted surface waters, and it is at this time of year that the annual primary production and chlorophyll a concentration reach their maximums (DE LEON & BRAUN, 1973). Although chlorophyll a and primary production values are higher in winter than at any other time of the year in this subtropical region, the values are lower than typical maxima observed in temperate areas during the spring bloom (HARVEY et al 1935; SVERDRUP, 1953).

The world's oceans are being affected by the global warming scenario that is bringing rapid changes to the Earth's environments (HOEGH-GULDBERG & BRUNO, 2010). For example, the average temperature of the upper layers of the ocean have increased by 0.6 °C over the past 100 years (PACHAURI, 2007) and the annual primary production of the world's oceans has decreased by at least 6% since the early 1980's (GREG et al 2003). Local and temporal events such as seasonality, variations of temperature and nutrients availability can be useful tools to predict the ocean response to climate change.

In this paper we studied the temporal and spatial distribution of production, biomass and size structure of phytoplankton in two separate coastal stations during two distinctive time periods: a warm period (2003-2005) and a cool period (2007-2008) based on sea surface water temperature. The two stations are in shallow water subtidal areas and are impacted by different degrees of anthropogenic influence; Boca Cangrejo (BC) is located in an urban area with marine outfalls in the vicinity while AB (Abades) is in a more isolated area where no marine outfalls are present. Our goals were:

1. To determine the contribution of ppp to total primary production and biomass in these two coastal shallow areas during the seasonal phytoplankton cycle.
2. To determine the effect of the location (related with the level of anthropogenic influence) on the biomass and production of picoplankton and the bigger than 2 mm phytoplankton community.
3. To determine the influence of time period (water temperature) on the biomass and production of picoplankton and the bigger than 2 mm phytoplankton community.

## 2. MATERIALS AND METHODS

Two shallow waters stations (4 to 6 meters depth) in the subtidal area were chosen on the south-eastern coast of Tenerife Island, Abades (AB; 28°08'26"N, 16°26'04"W) and Boca Cangrejo (BC; 28°24'22" N, 16°18'52"W) (Fig.1). Current and wind regimes are similar in both localities. Nevertheless, Abades has high densities of small individuals of the sea urchin species *Diadema africanum* and low macro-algal cover, usually called "urchin barren grounds", and Boca Cangrejo has low densities of large individuals and



high macro-algal cover. Both stations were sampled for fractionated chlorophyll a (bigger and smaller than 2 mm fractions) and fractionated primary production during two time periods: from October 2003 to April 2005 and from February 2007 to April 2008. AB was said to have a relatively low anthropogenic influence since it is located approximately 500 m from any residential areas. BC is located within a residential area built on the seashore, near some densely populated urban centres. BC also has marine outfalls in its vicinity whereas there are none at AB, suggesting that BC may be subject to local enrichment processes due to additional nutrient input to the marine environment.

The samples were taken monthly during the period covering the years 2003 to 2005. From 2007 to 2008 it was not possible to make monthly samplings and some periods of the year are absent.

Water samples were collected from the sea surface using polyethylene bottles. From each bottle, subsamples were drawn for chlorophyll a analysis and primary production measurements. Temperature was measured in situ with a portable thermometer.

### **2.1. *Pigment Concentration***

Chlorophyll a and phaeopigment concentrations were estimated with a Turner Designs Trilogy fluorometer equipped with an acidification method Chl a module and calculations used the equations from STRICKLAND & PARSONS (1972). For each sample, a 1000 ml subsample was filtered on a Millipore polycarbonate 2 mm filter to retain the fraction of phytoplankton cells greater than 2 mm, and another 1000 ml subsample was filtered on a Whatmann GF/F glass microfiber filter to retain the total phytoplankton population. Pigments were extracted in 90% acetone for 24 h in the dark at 4 °C. The picoplankton pigment concentration was calculated as the difference between the total and 2 mm fractions.

### **2.2. *Primary Production***

Primary production was measured using the  $^{14}\text{C}$  method of STEEMAN-NIELSEN (1957) using clear and dark polycarbonate bottles. 4 mCi of  $^{14}\text{C}$  in bicarbonate form were added to each bottle prior to incubation for 4 to 5 hours. After incubation, each bottle was filtered sequentially through filters with pore sizes 2 and 0.7mm (Whatmann GF/F glass microfiber filters). Filters were dried, fumed overnight with HCl and placed in scintillation vials with 8 ml of Optiphase Hi-Safe scintillation cocktail and measured in a liquid scintillation counter.

### **2.3. *Data Analyses***

A three way permutational ANOVA was used to analyse chlorophyll a concentration for phytoplankton cells larger than 2 mm, chlorophyll a concentration for phytoplankton cells smaller than 2 mm (photosynthetic picoplankton), and primary production of both photosynthetic picoplankton and bigger than 2mm photosynthetic cells. The factor 'year' was treated as a fixed factor with two levels ('warm' and 'cold'). 'Anthropogenic influence' was treated as a fixed factor with two levels ('AB' with low anthropogenic influence, and 'BC', with high anthropogenic influence). 'Period', referred to period of the year, was a fixed factor with two levels: 'stratified water column period' (from May to November) and 'mixed water column period' (from January to April).



The software PRIMER 6 and PERMANOVA + were used for all analyses of variance (ANDERSON *et al.* 2008).

### 3. RESULTS

The annual mean sea surface temperature (SST) cycle in AB during 2003 - 2005 showed its maximum during September - October (24.1 °C in October 2003 and 24.9 in September 2004), while the minimum values were measured in winter (19.20 °C in March 2004 and 19.0 °C in January, February and March 2005). BC showed a similar pattern during the same period (24.70 °C in September 2004, 24.20°C in October 2003, 19.00 °C in January 2005 and 19.60°C in March 2004). In the period within February 2007 and April 2008 the temperature maximum was detected in September (23.3 °C in both stations) and the minimum was detected in March 2007 (19.05 °C) and in February 2008 (19.7 °C). This annual temperature cycle corresponds well with previous works in the Canary Islands region (DE LEON & BRAUN, 1973; BARTON *et al.* 1998).

Mean SST during the 2003 - 2005 in the Canary Islands region was 21.51 °C, while during 2007-2008 it was 21.34 °C. Also, the highest SST of each year was higher during 2003-2005 than during 2007-2008 (Fig. 2). Because of these differences in SST between periods we decided to characterise 2003-2005 as a 'warm period' and 2007-2008 as a 'cold period'.

Analysis showed that the total chlorophyll a concentration at BC was higher than at AB in both warm and cold periods (Table 1, Fig. 3a). The mean [Chla] at BC was 44% higher than the value obtained at AB during the same time period (2003-2005). In the cold period (2007-2008) [Chla] at BC was 33% higher than the value at AB. Primary production was significantly higher at BC during both time periods (Table 1; Fig. 3b). Mean primary production at BC was 37% higher than at AB during the warm period and in the cold period it was 52% higher at BC than at AB. These results suggest that BC is more productive and supports a larger biomass of phytoplankton than AB, so the conditions are less oligotrophic in BC.

The [Chla] of cells >2 mm was higher in BC (Table 1; Fig. 3c). No significant difference in [Chla] of ppp was observed between the two stations.

#### 3.1. Temporal Variation

Photosynthetic picoplankton production showed significant differences between the two time periods sampled. At AB in particular production from ppp was higher during the cold period (Table 1, Fig. 3d). The difference in productivity of ppp was not accompanied by any significant differences in [Chla] from this fraction between warm and cold periods.

Photosynthetic picoplankton [Chla] in BC was higher during the warm period and [Chla] was dominated by the larger phytoplankton cells during the cold period at this site.

Production of phytoplankton >2 mm was greater at late winter, when the seasonal thermocline is usually absent in the Canary Islands (BRAUN, 1980; BARTON *et al.* 1998).

### 3.2. Warm Period in the Low Anthropogenic Influence Site (AB)

[Chla] peaked at  $0.27 \text{ mgm}^{-3}$  (compared to a mean value of  $0.18 \pm 0.06 \text{ mgm}^{-3}$ ); the highest [Chla] values were all obtained during the winter months: February 2004 ( $0.26 \text{ mgm}^{-3}$ ) and December, January and February of 2005 ( $0.24$ ,  $0.27$  and  $0.26 \text{ mgm}^{-3}$  respectively).

The mean ppp [Chla] was  $0.08 (\pm 0.05) \text{ mgm}^{-3}$ , the lowest value was  $\sim 0 \text{ mgm}^{-3}$  and maxima was  $0.20 \text{ mgm}^{-3}$ . This maximum [Chla] value was measured in November 2003 when the contribution of ppp to total [Chla] was of 76.9%. The contribution of ppp to the total phytoplankton [Chla] fluctuated during this period; with a mean of 39.5% ( $\pm 22.6\%$ ).

The maximum production occurred in October 2004 ( $0.98 \text{ mgCm}^{-3}\text{h}^{-1}$ ) although lesser peaks occurred in the winter months. Autumn peaks with higher production values ( $2.44 \text{ mgCm}^{-3}\text{h}^{-1}$  in October 2004) also occurred at BC providing further evidence that the high production values were not just an episodic event.

Levels of primary production showed greater temporal variation than [Chla]. Higher production rates were obtained in the winter months compared to spring or summer (there was an additional peak in autumn). Mean primary production was  $0.49 (\pm 0.21) \text{ mgCm}^{-3}\text{h}^{-1}$ .

Autotrophic picoplankton was responsible for 51.0% ( $\pm 12.7$ ) of total primary production at AB during the warm period, suggesting that microbial processes are important in this site. The mean ppp production in this period was  $0.28 (\pm 0.16) \text{ mgCm}^{-3}\text{h}^{-1}$ . However in January 2005 primary production by ppp peaked at  $0.52 \text{ mgCm}^{-3}\text{h}^{-1}$  and this group made up 62.7% of total production. In the October 2004 production peak the contribution from ppp was  $\sim 50\%$ .

### 3.3. Warm Period in the High Anthropogenic Influence Site (BC)

Mean total [Chla] was  $(0.32 (\pm 0.14) \text{ mgm}^{-3})$ , a value typical of oligotrophic areas. Although [Chla] was higher at the end of winter (February), an important [Chla] peak was measured in October ( $0.72 \text{ mgm}^{-3}$ ).

Photosynthetic picoplankton contributed less than 50% overall to total phytoplankton [Chla] at BC ( $44.5\% \pm 16.0$ ); mean ppp [Chla] was  $0.13 \pm 0.05 \text{ mgm}^{-3}$ . The main ppp [Chla] peak occurred in February 2004, when the group made up 63.4% of the total phytoplankton biomass.

Production showed high seasonal variation (mean  $1.07 \pm 0.52 \text{ mgCm}^{-3}\text{h}^{-1}$ ). Higher values were generally obtained in the late winter months (mean  $1.37 \pm 0.21 \text{ mgCm}^{-3}\text{h}^{-1}$ ) and lower values in summer (mean  $0.76 \pm 0.27 \text{ mgCm}^{-3}\text{h}^{-1}$ ), but the highest peaks occurred in autumn (maximum  $2.44 \text{ mgCm}^{-3}\text{h}^{-1}$  in October 2004). Primary production values this high are not normally expected in the Canaries during autumn; previously such levels have only been measured during the late winter-spring bloom.

Picoplankton contributed 48.8% ( $\pm 11.1$ ) to total primary production during the warm period at BC. At their peak in October 2004, ppp provided  $1.22 \text{ mgCm}^{-3}\text{h}^{-1}$ , making up 50% of total production.

### 3.4. Cold Period in the Low Anthropogenic Influence Site (AB)

[Chla] peaked in February 2008 ( $0.49 \text{ mgm}^{-3}$ ) and mean total [Chl a] was  $0.24 (\pm 0.12) \text{ mgm}^{-3}$ .

Photosynthetic picoplankton Chla concentration peaked in January and February 2008 and the mean for this group was  $0.08 (\pm 0.06) \text{ mgm}^{-3}$ . In February and March some



measurements showed that ppp [Chl a] was close to zero and overall the contribution of picoplankton to total [Chl a] was low at this site (32.6% ( $\pm 27.41$ )). Photosynthetic picoplankton made up the largest percentage of total phytoplankton [Chl a] in August 2007 (71.1%) when it was particularly low (0.14 mgm<sup>-3</sup>, see Fig. 4b).

At AB, mean total primary production was higher than at BC (0.72 ( $\pm 0.37$ ) mgCm<sup>-3</sup>h<sup>-1</sup>) and values rose above 1.00 mgCm<sup>-3</sup>h<sup>-1</sup> in September 2007 and February 2008. Also in February 2008 the contribution of ppp to total production was higher than at any other time during the cold period (ppp production was 0.85 mgCm<sup>-3</sup>h<sup>-1</sup>m), equivalent to 70.52% of total production compared to a cold period average of 14% ( $\pm 12.64$ ).

### 3.5. Cold Period in the High Anthropogenic Influence Site (BC).

In February 2008 total [Chl a] peaked at BC (0.90 mgm<sup>-3</sup>), the highest [Chl a] peak recorded during the present study. In the same month photosynthetic picoplankton [Chl a] was relatively low in comparison (0.10 mgm<sup>-3</sup>). Picoplankton contribution to total [Chl a] in BC was also low (mean = 17.34%  $\pm 22.0$ ): during several months of the cold period, chlorophyll a levels from the <2 mm cell fraction were undetectable.

Primary production at BC was high, exceeding 1.00 mgCm<sup>-3</sup>h<sup>-1</sup> in most of the sampled months, and mean total primary production was 1.15 ( $\pm 0.39$  mgCm<sup>-3</sup>h<sup>-1</sup>). Primary production by ppp (0.60  $\pm 0.22$  mgCm<sup>-3</sup>h<sup>-1</sup>) made up ~50.0% of the total.

## 4. DISCUSSION

The two time periods studied showed significant differences in ppp production and biomass. The higher biomass from small cells present in BC during the warm period is consistent with previous studies that have shown that warming decreases the size of individual phytoplankton (Morán et al. 2010). This occurred only in BC, which was more productive and rich in biomass than AB.

The temporal distribution of primary production and [Chl a] observed in this study showed some differences with the typical annual production cycle in waters around the Canary Islands unaffected by the NW African coastal upwelling. Phytoplankton are known to bloom in late winter in these waters when the seasonal thermocline is eroded allowing nutrient rich deep water layers to mix with nutrient depleted surface waters (BARTON *et al.* 1998). In the present study additional production peaks were observed in October 2003 and October 2004 at one of the study sites (BC). Such high rates of primary production were not expected during autumn due to the extent of stratification existing in the water column at this time of year. These peaks may have resulted from episodic inputs of nutrients from the land. Monthly precipitation data from the Spanish 'Agencia Estatal de Meteorología' (State Meteorological Agency) show that precipitation levels were particularly high in October 2003 and September 2004. The high level of rainfall may have contributed to more nutrients being leached from the land into the coastal sea. It has previously been observed that coastal environments are associated with complex phytoplankton dynamics because they are subject to different sources of nutrient input, turbulence, predators and light sources compared to open ocean populations (CABRIAS & VALIELA, 1999). In coastal environments phytoplankton also receive constant nutrient input from the terrestrial environment



or from the benthos which helps to maintain primary production throughout the whole year (DUGDALE & GOERING, 1967).

By comparing the two sites (BC and AB), differences can be seen in both total [Chl a] and total primary production. It is suggested that these differences are caused by the differing levels of anthropogenic influence at the two sites; at BC which is closer to a residential area and several marine outfalls total primary production of photosynthetic cells was greater. The additional anthropogenic nutrient input (from the marine outfalls) may have been responsible for the higher levels of primary production in both the  $>2$  and  $<2$  mm photosynthetic cell fractions at BC compared to AB. However, [Chl a] was only higher at BC in the larger cell fraction ( $>2$  mm). In oceanic oligotrophic waters, picoplankton tends to dominate phytoplankton biomass (CHISHOLM, 1992; PARTENSKY *et al.* 1996; AGAWIN *et al.* 2000; BELL & KALFF, 2000). The locations sampled in the present study are situated in shallow coastal waters (5 to 10 meters depth) where higher levels of nutrient input can be expected compared to open ocean.

Previous studies have suggested that an increase in nutrient input stimulates production of both autotrophic picoplankton and larger phytoplankton cells, the relative importance of the microbial food web is thought to decrease under higher nutrient conditions since larger phytoplankton come to dominate total biomass (BELL & KALFF, 2001).

The results of the present study were in keeping with BELL & KALFF'S finding as larger cells did dominate biomass at both coastal sites. Ppp made up  $>50\%$  of total primary production in both study periods but the [Chl a] (proxy of biomass) of these small cells was lower at BC than at AB (17.34% of total compared to 32.57%).

In more productive waters the biomass of larger phytoplankton has been found to exceed that of picoplankton (AGAWIN *et al.* 2000). The contribution of ppp to total phytoplankton may have therefore diminished under higher eutrophication levels. Since BC is the more anthropogenically impacted of the two sites, it is suggested that the relative dominance of larger phytoplankton cells may be a result of a higher level of nutrient input. It has also been observed that primary production and [Chl ] are uncoupled. An increase in ppp production did not always translate to an increase in ppp [Chl a], perhaps due to the high level of grazing pressure that exists on picoplankton in coastal waters richer in nutrients. Macrozooplankton grazing is a significant factor determining mortality of phytoplankton in the oceans (CALBET & LANDRY, 2004) and ingestion rates increase nonlinearly as primary production increases (CALBET, 2001). Previous studies have also shown that larger phytoplankton cells can grow faster when nutrients are available (CHEN & LIU, 2010). It has also been observed that in high nutrient conditions the grazing pressure is higher on smaller cells (BARQUERO *et al.* 1998; WATSON & MCCAULY, 1988, CALBET, 2001; CALBET, 2008) whilst the size of larger phytoplankton proves an effective grazing deterrent (LITCHMAN *et al.* 2007). This differential grazing effect and its effect on biomass accumulation could also explain why production was higher at BC than AB in both large and small cell fractions whereas differences in biomass were only detected in the  $>2$  mm fraction.

The close proximity of BC to a residential area and marine outfalls probably enhanced total phytoplankton productivity and biomass at this site. This may be caused by a higher nutrient input from anthropogenic sources but, unfortunately, although water samples were taken for nutrients measurements, it was not possible to analyse these

samples. Productivity was higher in both size fractions of photosynthetic cells (<2 mm and >2 mm). [Chl a] of the photosynthetic picoplankton did not differ significantly between the two stations.

Primary production by photosynthetic picoplankton dominated total production (> 50% of total) but the percentage contribution of this fraction to total biomass was lower under the less oligotrophic conditions associated with BC.

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**Table I.-** Three-way Permutational ANOVA showing the effect of year, anthropogenic influence and period on total and fractionated chlorophyll a concentration and total and fractionated primary production.

| <i>a. Total Chl a</i>              |    |           |           |        |
|------------------------------------|----|-----------|-----------|--------|
|                                    | df | MS        | Pseudo-F  | P (MC) |
| ye                                 | 1  | 1,495E-2  | 1,2122    | 0,316  |
| ai                                 | 1  | 0,13659   | 11,623    | 0,007  |
| pe(ye)                             | 2  | 9,2276E-3 | 0,4314    | 0,667  |
| yexsi                              | 1  | 1,9367E-3 | 0,16479   | 0,688  |
| pe(ye)xsi                          | 2  | 8,4471E-3 | 0,39491   | 0,654  |
| Res                                | 45 | 2,139E-2  |           |        |
| Total                              | 52 |           |           |        |
| <i>b. Chla &lt;2</i>               |    |           |           |        |
| ye                                 | 1  | 1,1877E-2 | 9,0573    | 0,01   |
| ai                                 | 1  | 3,5834E-3 | 3,6248    | 0,07   |
| pe(ye)                             | 2  | 4,3786E-4 | 0,11349   | 0,885  |
| yexsi                              | 1  | 9,9865E-3 | 10,102    | 0,005  |
| pe(ye)xsi                          | 2  | 4,4598E-6 | 1,156E-3  | 0,998  |
| Res                                | 45 | 3,8581E-3 |           |        |
| Total                              | 52 |           |           |        |
| <i>c. Chla &gt;2</i>               |    |           |           |        |
| ye                                 | 1  | 6,5179E-2 | 6,1029    | 0,055  |
| ai                                 | 1  | 8,9229E-2 | 8,909     | 0,028  |
| pe(ye)                             | 2  | 8,7137E-3 | 0,53089   | 0,597  |
| yexsi                              | 1  | 2,6947E-3 | 0,26905   | 0,628  |
| pe(ye)xsi                          | 2  | 7,8215E-3 | 0,47653   | 0,626  |
| Res                                | 45 | 1,6413E-2 |           |        |
| Total                              | 52 |           |           |        |
| <i>d. Total Primary Production</i> |    |           |           |        |
| ye                                 | 1  | 0,17542   | 3,3791    | 0,086  |
| ai                                 | 1  | 2,6289    | 55,058    | 0,001  |
| pe(ye)                             | 2  | 1,7721E-2 | 0,11689   | 0,881  |
| yexsi                              | 1  | 6,4038E-2 | 1,3412    | 0,254  |
| pe(ye)xsi                          | 2  | 1,2127E-2 | 7,9988E-2 | 0,908  |
| Res                                | 45 | 0,15161   |           |        |
| Total                              | 52 |           |           |        |
| <i>e. Prod &lt;2</i>               |    |           |           |        |
| ye                                 | 1  | 0,12516   | 11,576    | 0,002  |
| ai                                 | 1  | 0,56958   | 26,453    | 0,001  |
| pe(ye)                             | 2  | 3,6244E-4 | 8,78E-3   | 0,995  |
| yexsi                              | 1  | 2,1108E-3 | 9,8033E-2 | 0,758  |
| pe(ye)xsi                          | 2  | 1,4758E-2 | 0,35752   | 0,696  |
| Res                                | 45 | 4,128E-2  |           |        |
| Total                              | 52 |           |           |        |
| <i>f. Prod &gt;2</i>               |    |           |           |        |
| ye                                 | 1  | 12,555    | 1,9787    | 0,171  |
| ai                                 | 1  | 16,332    | 10,072    | 0,001  |
| pe(ye)                             | 2  | 7,9294    | 4,5942    | 0,001  |
| yexsi                              | 1  | 5,5796    | 3,4409    | 0,056  |
| pe(ye)xsi                          | 2  | 1,5857    | 0,91877   | 0,442  |
| Res                                | 45 | 1,726     |           |        |
| Total                              | 52 |           |           |        |

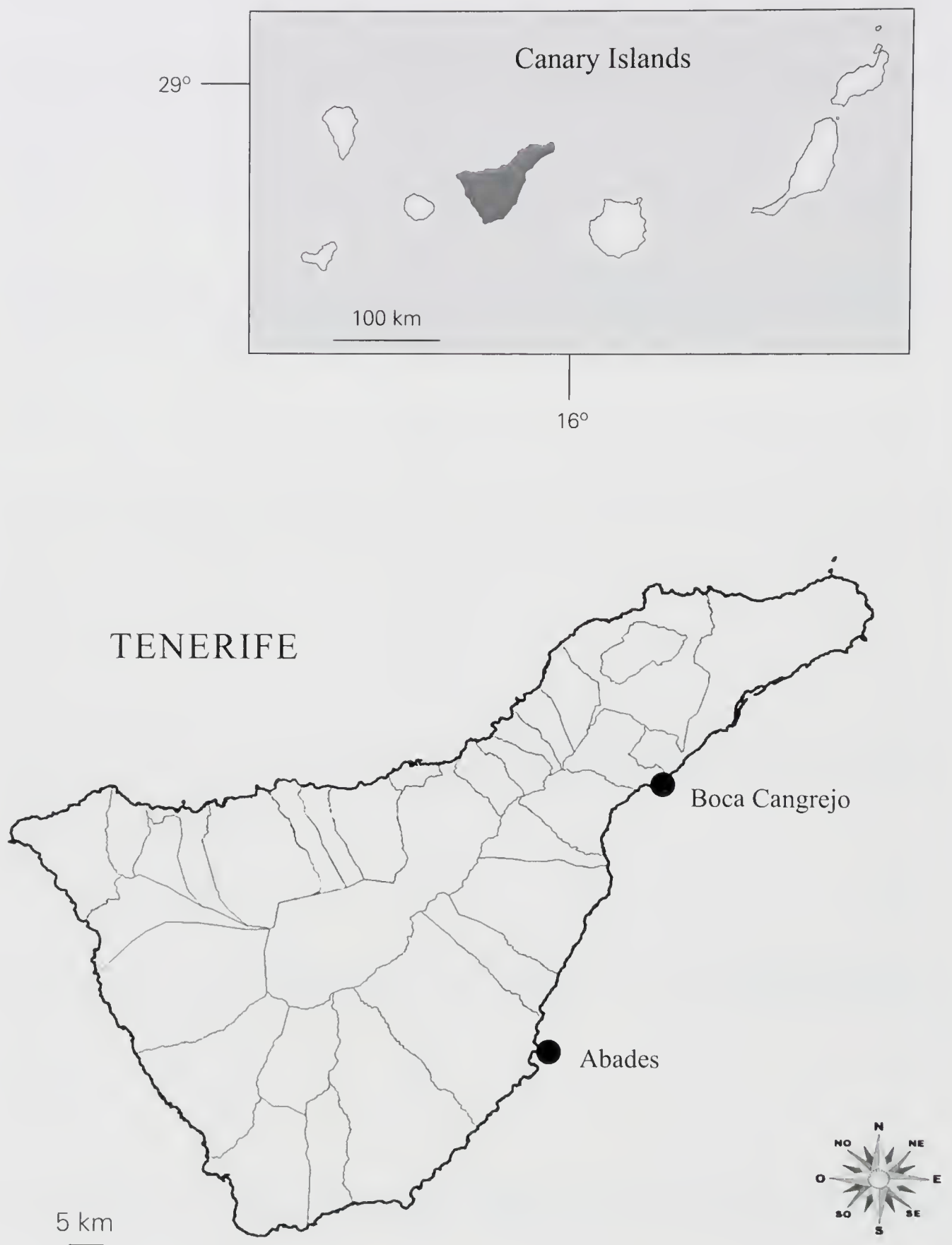
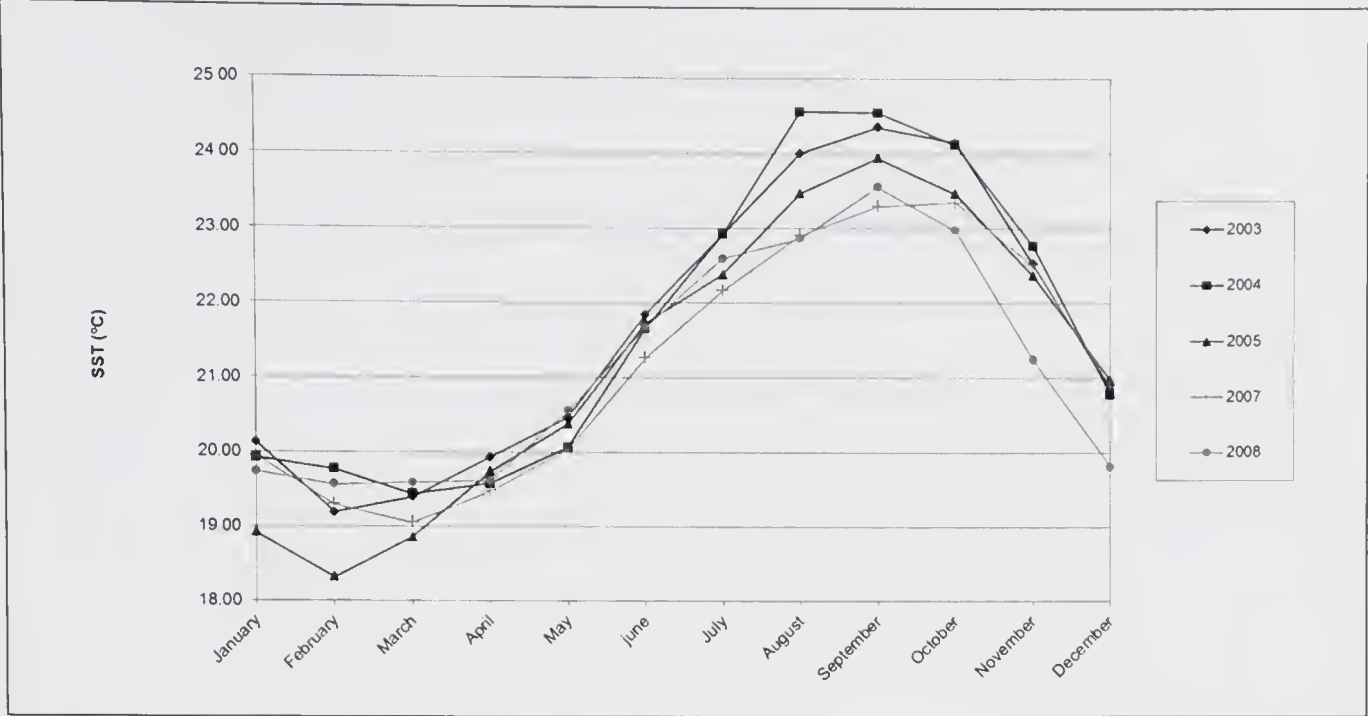
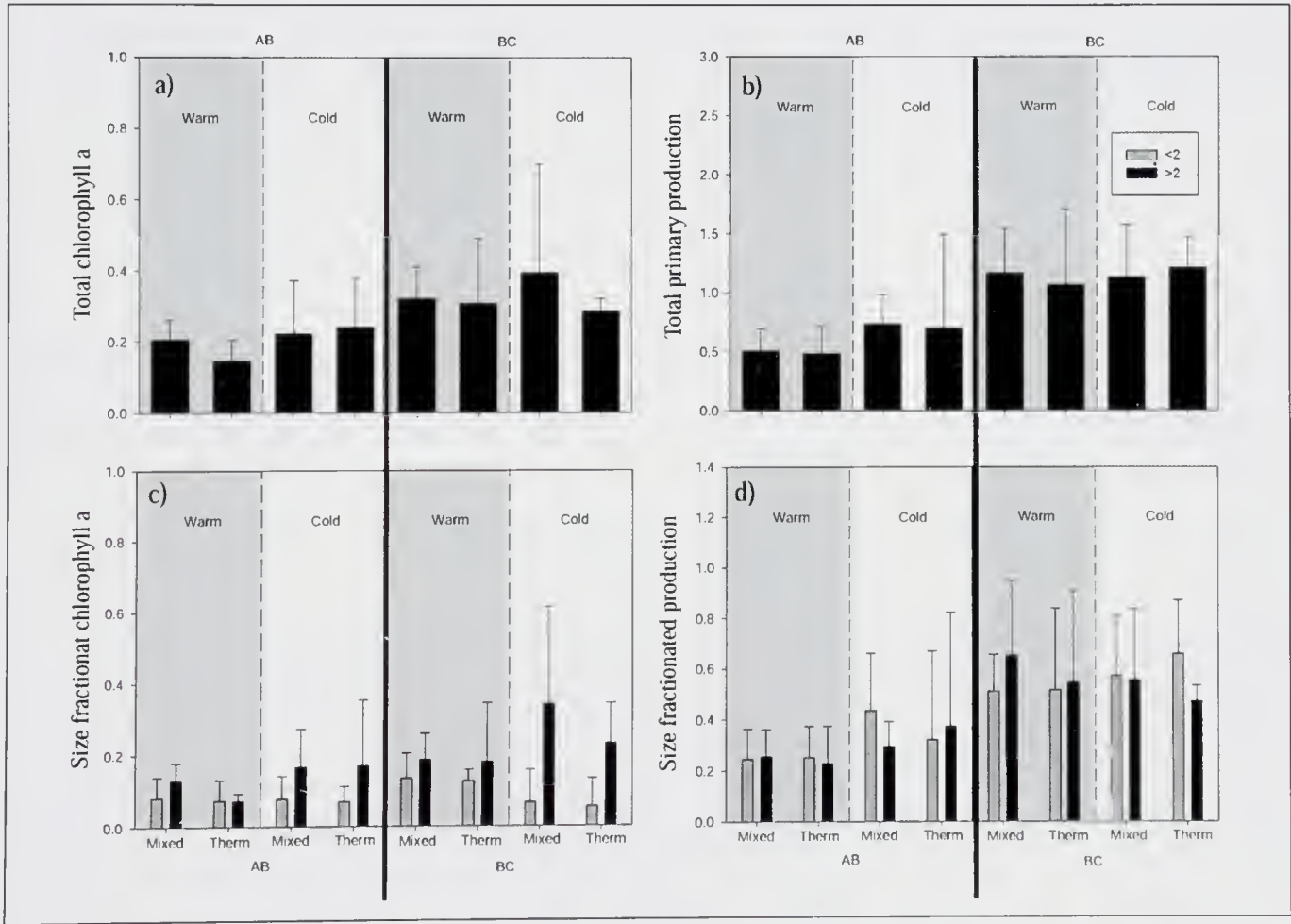


Figure 1.- The Abades and Boca Cangrejo locations in Tenerife.

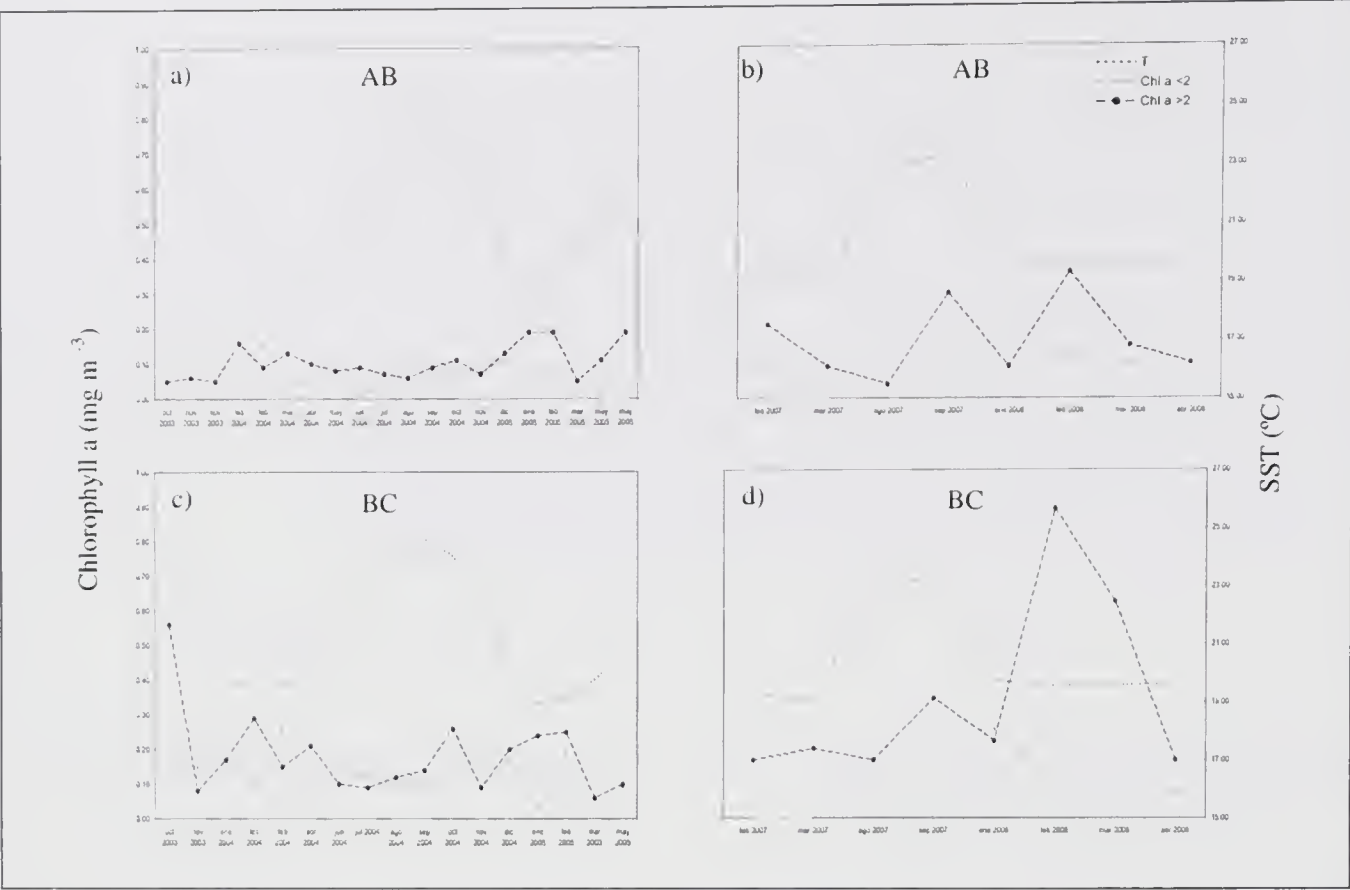




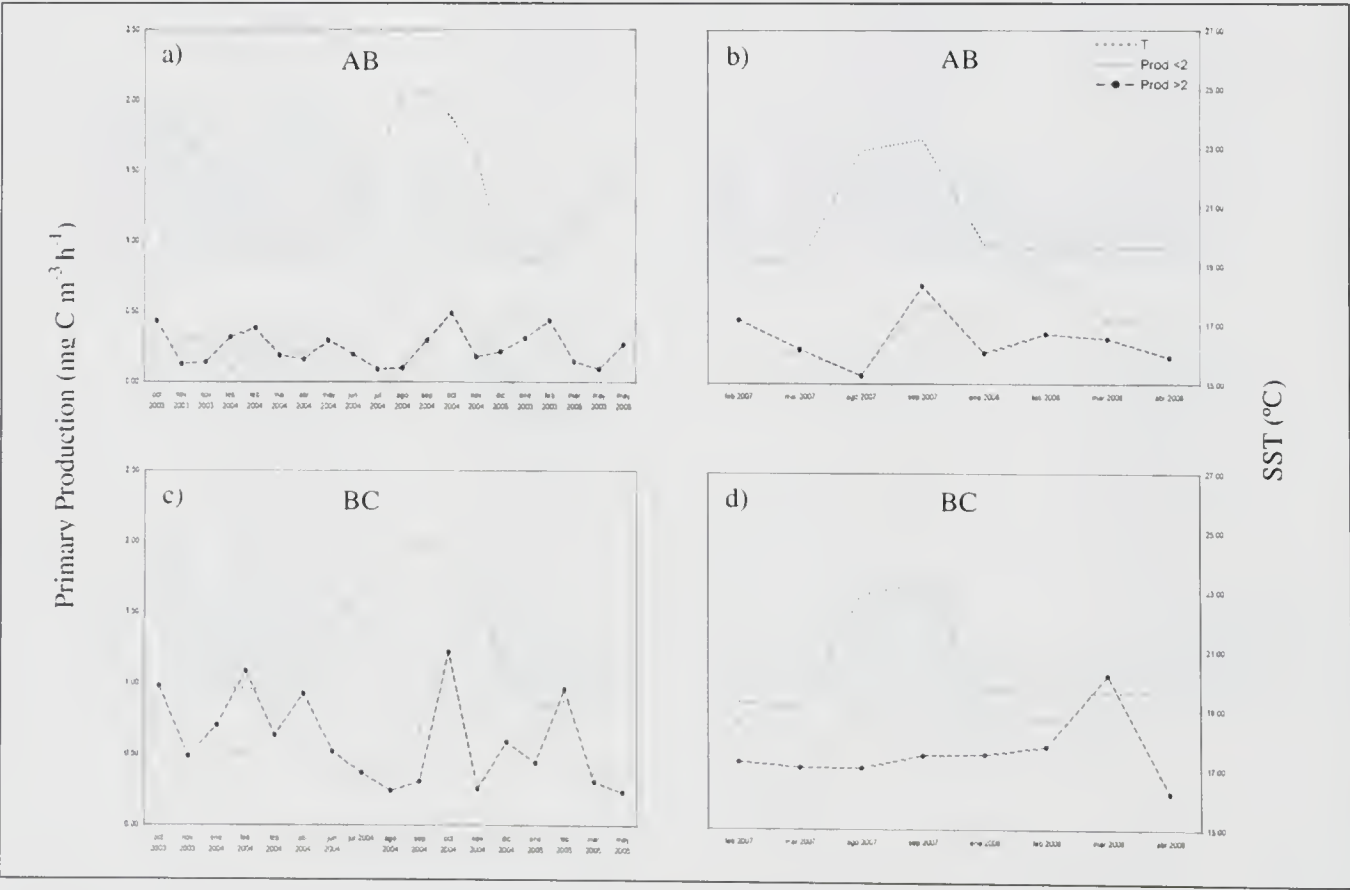
**Figure 2.-** Monthly mean Sea Surface Temperature in the Canary Islands from 2003 to 2008. Source:<http://www.esrl.noaa.gov/>.



**Figure 3.-** Mean values of chlorophyll a and primary production during the “warm” and “cold” periods in the two stations studied at the time of the year when the seasonal thermocline is present (‘Therm’) and when the seasonal thermocline disappears (‘Mixed’). (a) Total chlorophyll a (b) Fractionated chlorophyll a (c) Total primary production (d) Fractionated primary production.



**Figure 4.-** Seasonality of size fractionated chlorophyll a concentration: a) AB warm period b) AB cold period c) BC warm period d) BC cold period.



**Figure 5.-** Seasonality of size fractionated primary production: a) AB warm period b) AB cold period c) BC warm period d) BC cold period.